A Simulation Model of the Response of Harp Seals to Alternative Harvesting Strategies

Prepared for

Hon. John Efford
Minister of Fisheries and Aquaculture
Government of Newfoundland and Labrador
Fisheries Building
30 Strawberry Marsh Road
St. John's, NF

Prepared by

George H. Winters and Daniel S. Miller
Focus Technologies Inc.
33 Kenmount Road
St. John's, NF
A1B1W1

December 1998

Focus Technologies Incorporated

Table of Contents

1.0 INTRODUCTION 1
1.1 Background 1
1.2 Study Objectives 4
1.3 Data Sources and Analytical Procedures 5

2.0 ANALYSIS OF DENSITY-DEPENDENT VITAL RATES 8

3.0 CONSTRUCTION OF THE SIMULATION MODEL 13

4.0 RESULTS OF SIMULATION STUDY 16

5.0 DISCUSSION 23

6.0 SUMMARY 27

1.0 INTRODUCTION

Focus Technologies was contracted in November 1998 by the Newfoundland Department of Fisheries and Aquaculture to undertake a study of the likely population response of harp seals to alternative harvesting strategies. This report documents the results of this study. We acknowledge Dr. G. Stenson, Dr. P. Shelton and Dr. B. Sjare of the Department of Fisheries and Oceans, Newfoundland Region for their assistance in providing data and updating the harp seal population assessment model.

1.1 Background

The Northwest Atlantic harp seal (*Pagophilus groenlandica*) population has been commercially exploited since the 16 century (Coleman,1937; Barchard, 1978) with the most intensive exploitation occurring in the 19th century when the demand for skins in the luxury clothing trade initiated the development of a large fleet of schooners capable of penetrating the breeding areas in the Front area off northeastern Newfoundland (Chafe et al.,1923). An average of 450,000 pelts was harvested at the Front during the peak years of 1830-50, including a peak kill of nearly 700,000 pelts in 1844.The average harvest of pelts declined to slightly in excess of 300,000 animals for the latter half of the 19th century and declined further to about 150,000 animals between the two world wars. The seal hunt ceased almost entirely during the Second World War but intensified considerably after 1945 when Norway began sending vessels to the Front. From 1949 to 1971, when quotas were first introduced, the average kill was about 300,000 animals (Figure 1), declining to an average of 175,000 animals

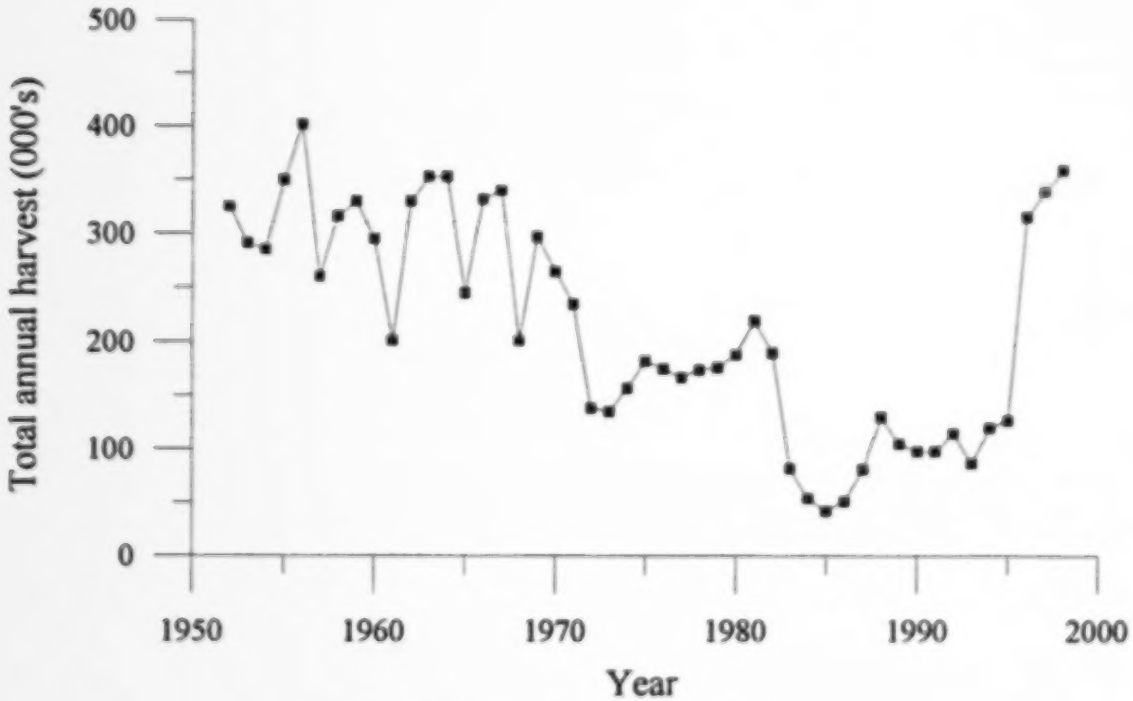

Figure 1. NW Atlantic harp seal catches 1952-98

until 1983 when markets collapsed because of the ban on the importation of whitecoat pelts by the EEC. Harvest levels remained low until 1996 when market forces resulted in harvest levels increasing dramatically to about 300,000 animals in 1996-98, including a much higher harvest of harp seals from West Greenland (Anon., 1998).

A variety of techniques have been used to estimate abundance of harp seals. These include the survival index method (Sergeant, 1971; Winters, 1978; Cooke, 1986), sequential population analyses (Lett and Benjaminsen, 1977; Winters, 1978), mark-recapture methods (Roff and Bowen, 1983; 1986) and direct surveys of pup production levels (Fisher, 1954; Sergeant, 1975; Stenson et al., 1996).The current assessment of harp seals (Shelton et al., 1996) is based on a population model that consists of matching the output of a simulation model with a set of independent observations of pup productions and time-dependent reproductive rates. A maximum likelihood procedure is then used to estimate the average natural mortality rate and size of the age 1+ population over a period of years. Population trends since 1952 are shown in Figure 2. It is clear that the harp seal population has made a dramatic recovery from depleted levels in the early 1970's and, at 5.4 million seals, is now at its highest level in recent history and perhaps since the mid 19th century (see later discussion). Concomitant with this increase in population size has been a substantial increase in prey consumption by harp seals to about 7 million tons (Stenson et al.,1997).

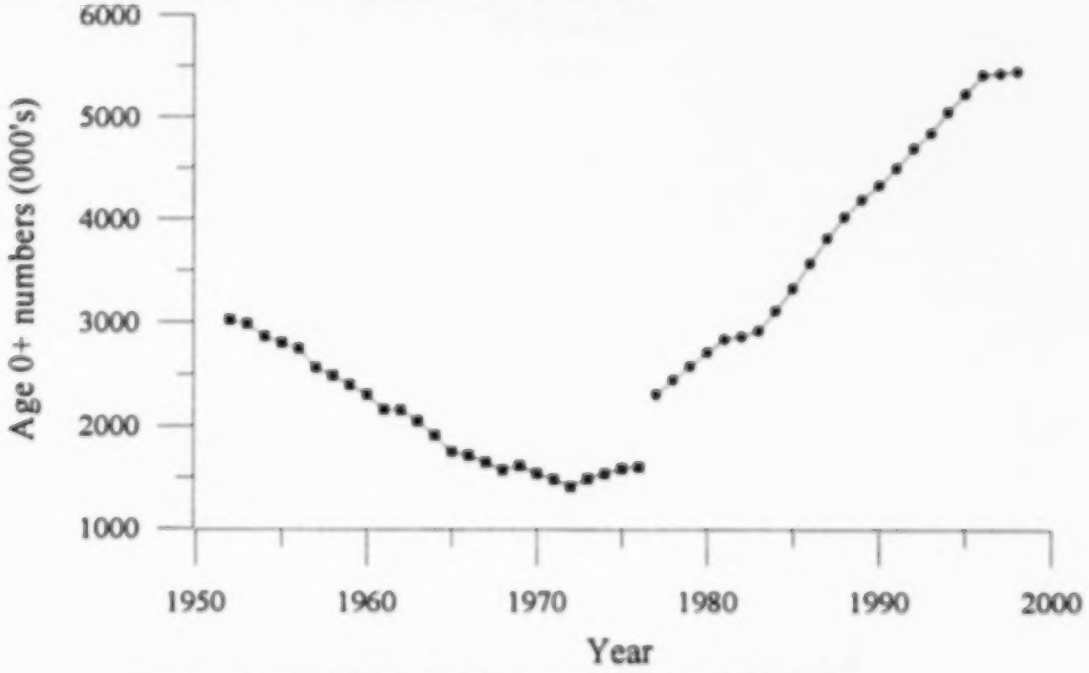

Figure 2. Population trends of age 0+ harp seals for the period 1952-98
The estimates for the years 1952-76 are from Winters (1978)
The estimates for the years 1977-98 are from Shelton et. al. (1996, revised)

The Northwest Atlantic harp seal population is currently regulated by a total allowable catch (TAC) which is set at the level of the replacement yield, defined as that level of catch which leaves the

numbers in the population at the end of the year the same as those at the beginning of the year. Replacement yield is a convenient management tool if the objective of management is to maintain herd size at some biologically or tactically defined optimum. The management strategy applied during the 1970's was to set the TAC at levels below the replacement yield until an interim target of 1.6 million animals age 1 and older was reached (Anon., 1979). This target was one estimate of the maximum sustainable yield (MSY) level for Northwest Atlantic harp seals. Given that the population size of harp seals has more than doubled over the past decade and that the 1 + population is now nearly 5.0 million, replacement yield may no longer be a suitable basis for managing harp seals. Furthermore, current management strategy appears to have no clear regulatory objective other than allowing the catch and population to interact in a haphazard fashion. In this report we consider, through simulation studies, the long-term equilibrium response of the harp seal population to a variety of alternative management strategies. Before doing so, a brief review of harp seal biology may be in order.

Harp Seal Life History Traits

The following account of harp seal biology is taken largely from Sergeant (1991).The harp seal (*Pagophilus groenlandica*) has a wide distribution throughout the subarctic waters of the north Atlantic where it reproduces in three widely separated breeding areas located in the pack ice in the White Sea, around Jan Mayen Island, and along the east coast of Canada which we shall refer to as the Northwest Atlantic harp seal population. Of these, the Northwest Atlantic herd is by far the largest in numbers. Taxonomic and tagging studies have shown that while there is a significant interchange between the White Sea and Jan Mayen herds (Yablokov and Sergeant, 1963; Sergeant, 1973), there is very little interchange between the Northwest Atlantic herd and the two populations in the Northeast Atlantic. The Northwest Atlantic population has two main breeding areas which are found in the Gulf of St Lawrence, and in the Front area off the coast of southern Labrador. There is considerable mixing between the Front and Gulf populations particularly as bedlamers (immatures) but the adults tend to return with some but not absolute fidelity (Winters, 1978) to their natal area.

Harp seals summer in Canadian arctic and along the west coast of Greenland. They begin their southward migration in early fall and by late November reach the southern Labrador coast where about a third of the mature seals enter the Gulf of St Lawrence and the remainder, including most of the immatures, migrate southwards along the east coast of Newfoundland. From December to February, intensive feeding takes place as the pregnant females increase their fat thickness in preparation for breeding which begins in late February in the Gulf, and about eight days later on the Front. The breeding season can extend for several weeks but most of the pups are born in a much shorter period of a week to ten days. The "whitecoat" pup is about 11 kgs at birth and has a long white coat of fur which is retained for about 2 ½ weeks. Growth rates are rapid during weaning and pups reach a weight of about 35 kgs at the beginning of whitecoat molt which takes about 10 days to complete and is referred to as the "raggedy jacket" stage. When the whitecoat molt is complete, the pups have a short spotted pelage and are commonly referred to as "beaters". After weaning the mothers abandon their pups and mate with one or males usually in the water.

At the Front, the beaters drift southwards with the pack ice and begin active feeding largely on zooplankton. In early April the immatures and adult males haul out on the receding pack ice to molt,

with the adult females molting about about two weeks later. The summer migration of these age groups to Arctic waters then begins with the beaters following about a month later. Most of the beaters and immature seals summer along the West Greenland coast with the mature seals feeding mainly in the Canadian Arctic. However, results from recent tagging experiments show that a significant number of mature harp seals also spend the summer and fall in West Greenland waters and that some of them remain there over the winter (Kapel, 1996).

In autumn, most harp seals leave the Arctic in a long Front just ahead of the formation of the local pack ice, with the older animals migrating first. Traditionally, harp seals were considered to be a nearshore inhabitant during their winter-spring residence in Newfoundland waters. Recently, however, satellite tagging studies show that harp seals have an extensive distribution across the southern Labrador Shelf and Grand Banks out to depths of 400 meters (Stenson and Sjarre, 1997). It is not known if this is normal or an exceptional distributional pattern resulting from the extensive cooling of ocean climate that occurred in the 1990's.

1.2 Study Objectives

In this report, the most recent estimates of population size and vital rates of Northwest Atlantic harp seals will be used to construct an age structured population model capable of simulating the response of harp seals to a variety of alternative harvesting strategies as well as estimating near-term yields. In its simplest form, the simulation model will assume that recent mortality and reproductive rates will prevail throughout the simulation period. However, the long-term response of harp seals to any of these harvesting levels will depend critically on the existence and intensity of density dependent mechanisms, which occur in many wild populations as a counterbalance to population change. To this end, all published data relevant to coincidental changes in vital rates and population size will be reviewed and empirical relationships estimated where statistically evident. The statistical expressions of density dependence will then be used as an alternative simulation model to estimate the MSYof harp seals, and the associated population size. Maximum sustainable yield is defined as the greatest harvest that can be taken from a self-sustaining stock of animals while still maintaining constant average size of the stock. The density-dependent model will also be used to reassess the population response of harp seals to the harvesting strategies outlined above. In particular, the simulation models will be used to answer the following questions with respect to short-term and long-term harvest strategies.

Question 1. What is the current replacement yield?

Question 2. What is the long-term response of the harp seal population if the hunt continues to be regulated at the current level of 275,000 seals?

Question 3. What is the long-term response of the harp seal population if the hunt is regulated at a level of 400,000 animals?

Question 4. What is the long-term response of the harp seal population to a one-time cull of 2,000,000 animals followed by a resumption of the current harvest of 275,000 animals?

Question 5. If a density-dependent function can be statistically demonstrated for the harp seal population, what is the Maximum Sustainable Yield and at what population size will this maximum occur? How does the existence of density-dependence affect the conclusions arrived at with respect to the alternative harvesting strategies outlined above? Further, in the absence of a hunt how much farther will the population expand?

1.3 Data Sources and Analytical Procedures

The population vector (Figure 3) used as a starting point for all simulations are the 1998 population numbers at age derived from the population assessment model of Shelton et al.,(1996), which was recently modified to include revised Greenland catches and the most recent reproductive rate data (Dr. G. Stenson, p. com.). The simulation model will be stochastic in the sense that certain population statistics, such as the 1998 population size and natural mortality, will be drawn from error probability distributions as defined in the output of the statistical model used to estimate natural mortality and 1+ population sizes. Warren et al., (1997) have shown that the asymmetrical confidence limits derived by Shelton et al., (1996) exhibited strong negative skewness and underestimated the true variance, and that symmetric confidence limits were more appropriate. We have consequently used the variance statistics given in Warren et al., (1997) as the basis for our random number seed and, have further assumed that the coefficient of variation for the 1+ age-groups is the same as that estimated for the pups. Shelton et al., (1996) provide two formulations of mortality schedules when fitting their model to estimated pup levels; one in which pup mortality was assumed to be the same as that for all the older age-groups and one in which pup mortality was assumed to be three times that of the older age-groups. Since the differences in the estimates of population size are inconsequential (Warren et al., 1997), we have used the population statistics from the former model only. In addition, the absence of a significant number of predators and the low incidence of dead or dying pups on the ice suggest that natural mortality of harp seal pups may be low (Sergeant, 1991) and the same as that estimated for the older age-groups (Winters, 1978).

Shelton et al. (1996) provide estimates of age-specific population numbers for ages up to age 12 only, with the older animals being grouped into an age 13+ age group. Since harp seals are known to have a life span of at least 30 years (Sergeant, 1991) we prorated the age 13+ age-group to age 30 using an exponential decay model with total mortality set at 0.10. Cohorts were extirpated after age 30.

Catch-at-age data used in all projections assume that pups comprise 75% of the total catch, consistent with recent statistics for this ratio for 1996-98. This ratio will affect the estimates of harvest levels; in general, lower yields can be expected with a higher ratio of age 1 + animals in the catch. Annual catch at age compositions for the older age groups have been calculated from the appropriate population vector using a smoothed age-specific selection curve derived from the pattern of hunting mortalities by age for the period 1990-93 (Figure 4). This selection is consistent with similar curves calculated by Winters (1978) and Lett and Benjaminsen (1997) for earlier periods of the hunt.

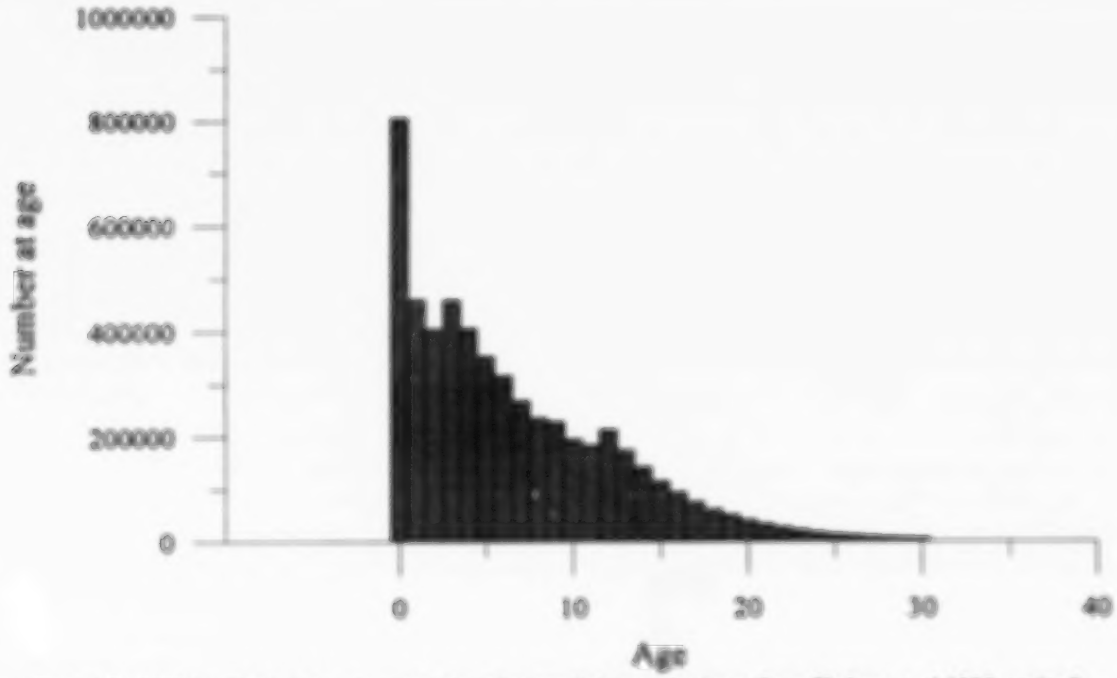

Figure 3. 1998 population at age used to start the population projections (from Shelton et. al 1996, revised)

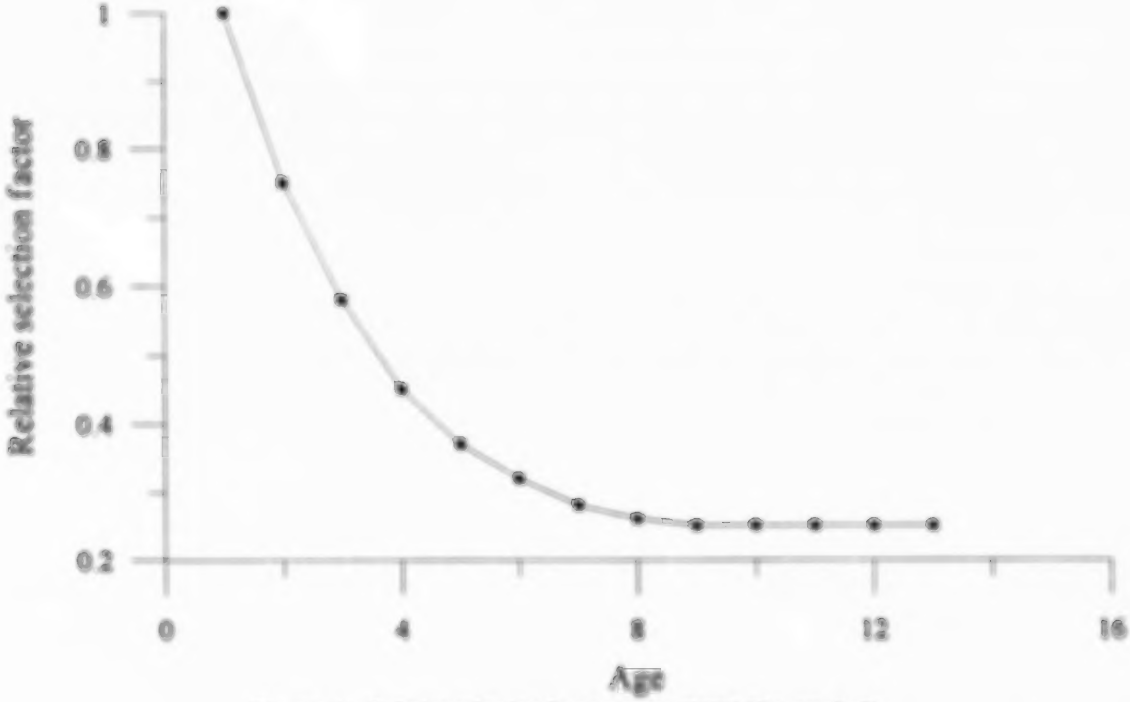

Figure 4. Relative selection factors at age (1990-91 smoothed)

A variety of authors have suggested that certain vital rates (eg., maturity rate, fertility rate and natural mortality rate) of Northwest Atlantic harp seals are density dependent (Sergeant, 1973, 1976 1978, Winters, 1978, Lett and Benjaminsen, 1977, Bowen et al., 1981). That is to say, such rates respond inversely to changes in population abundance. The historical relationships, however, were based on very few data points and depended very heavily on meager and uncertain data describing changes in vital rates during the monotonic decline in population numbers from the early 1950's to the 1970's. Since then, the harp seal population has recovered from the low levels of the early 1970's and has gone well beyond those estimated for the 1950's (Figure 2). The timing is now propitious for a reexamination of recent reproductive data to ascertain whether or not the changes which occurred during the population decline, have shown a commensurate reversal as the population increased to current high levels. Our approach will follow along the same general procedures used by Lett and Benjaminsen (1977) and Lett et al., (1979). We have used, as our data sources for mean age at maturity and fertility rates for the years prior to 1980, estimates of these parameters provided in Bowen et al 1981. These data are, for the most part, sufficiently well sampled to provide annual estimates of mean age at maturity and fertility. The more recent data are generally poorly sampled on an annual basis but are statistically adequate when pooled across years. We have therefore used the pooled estimates for 1985-89 and 1990-94 as given in Sjare et al., (1996). Our analyses include both early term (April) and late term (winter) maturity data as there was no compelling reason not to. However, we have restricted our analyses of maturity data to Front samples only. This is because the Gulf of St Lawrence samples, particularly those from the North shore of Quebec, are known to be deficient in immature seals during the fall-winter migration period (Sergeant, 1977). In all cases, the mean age of maturity has been advanced one age to the year of parturition i.e., the age of reproductive maturity. Sex ratios are assumed to be 50:50 in all cases.

Fertility rate defined as the proportion of mature females that are pregnant at the time of the sample are for late term only since early term rates are essentially ovulation rates and should not be combined with late term rates. Annual estimates of this parameter for the years prior to 1980 are given in Bowen et al., (1981) and pooled estimates for the period 1985-89 and 1990-94 are given in Sjare et al., (1996).

Lett et al., (1979) concluded that the natural mortality rate of pups surviving the whitecoat hunt was density-dependent. This conclusion was based on a comparison of the number of one year old animals estimated from sequential population analyses, with estimates of pup production calculated from reproductive rates applied to annual population numbers estimated from the same sequential population estimates. The conclusion of Lett et al., (1979), however, depends critically on the manner in which the selection pattern at age is chosen and a different selection pattern, such as that estimated by Winters (1978), does not give the same result. Further, the inverse relationship between pup kills and survival indices (Winters, 1978) could not exist if the natural mortality rate of pup escapements were density-dependent. For these reasons we have not included density-dependent pup mortality as a function in the development of the simulation model.

2.0 ANALYSIS OF DENSITY-DEPENDENT VITAL RATES

The analyses of mean age at reproductive maturity (***Mam***) changes requires, first of all, an evaluation of the pattern of change in the maturity ogive (***Mat***) itself, and whether or not changes in mean age are confounded by coincident changes in the shape of the maturity ogive ie. variation in the standard deviation. We checked for variation in the standard deviation of the maturity ogive by re-scaling the age of maturity to standard ages by subtracting the mean age of maturity for each period from the ages included in the maturity ogive (i.e. all ogives were standardized to zero). For these analyses we used the aggregated maturity data reported in Sjare et al.,(1996) for four time periods (1965-69, 1978-82, 1985-89, 1990-94) which covered major changes in population abundance. There was no indication that the standard deviation describing the rate of accumulation of mature animals in the population had changed. Arcsine transformations, constrained to the first quadrant, were used to linearize the cumulative normal distributions describing the maturity data for each period; these were also examined to determine whether the ogives could be superimposed on one another (Figure 5). No statistical differences were evident so the standardized maturity data were combined into a single maturity ogive described by the following algorithm (Figure 6, Table 1);

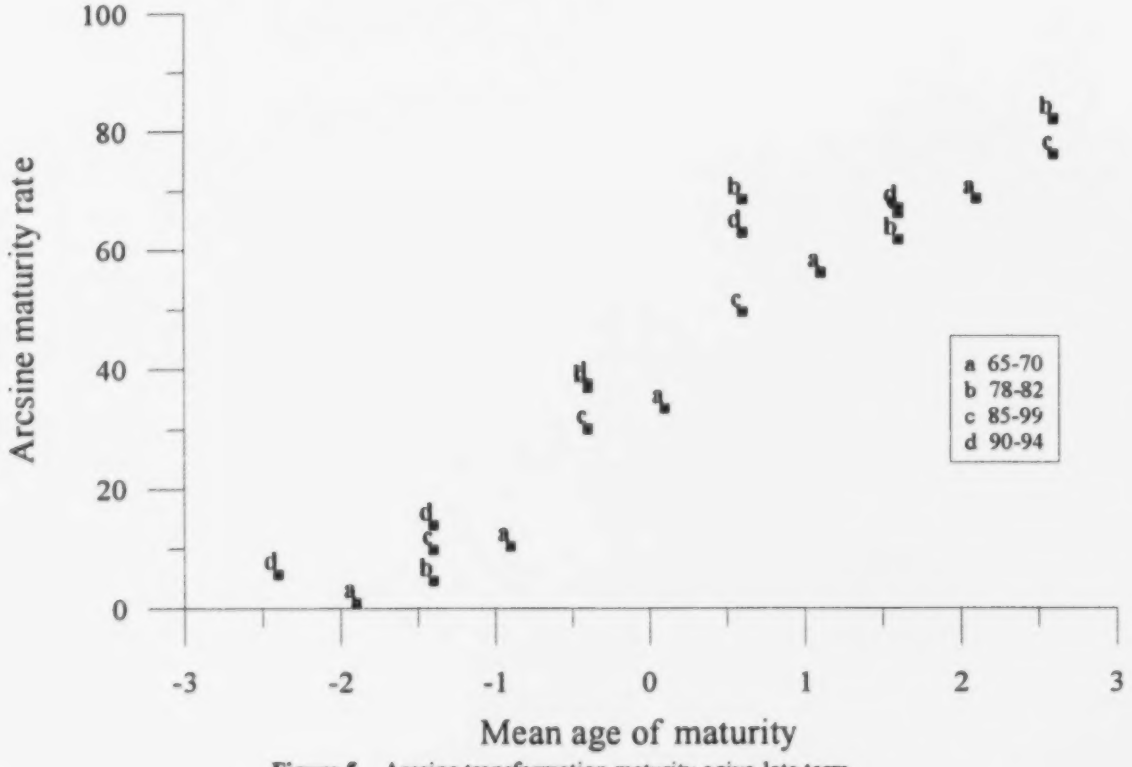

Figure 5. Arcsine transformation maturity ogive-late term.
Data from Sjare et al., 1996

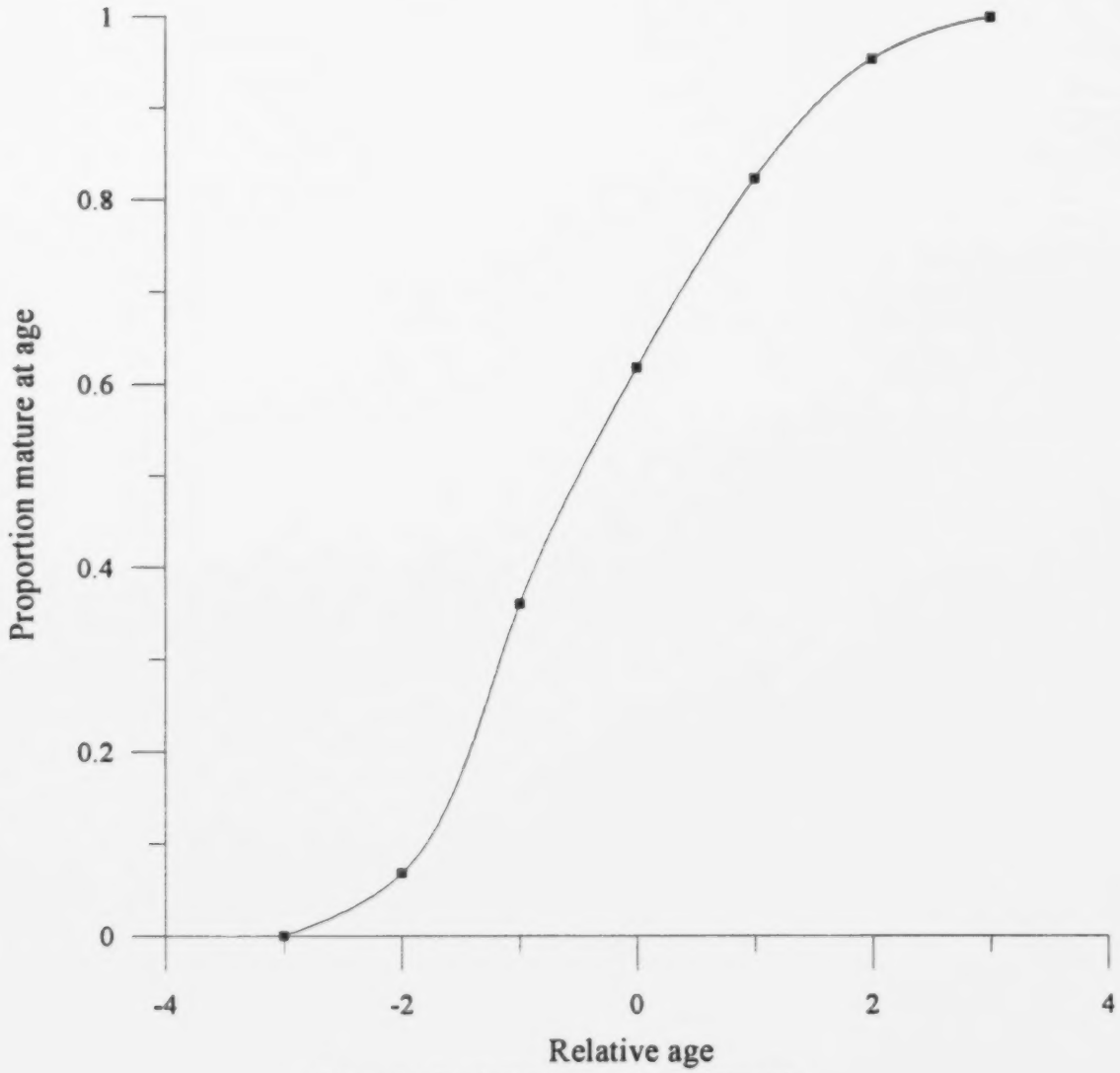

Figure 6. Standard maturity ogive for harp seals

$$(1)\quad Mat_a = \text{Sine}(38.2 + 17.1(a\text{-}Mam))$$

where: Mat_a is the age specific maturation for age a.
Mam is the mean age of reproductive maturity.
a is age.

To investigate the statistical expression of density dependence between mean age at maturity and population size we regressed estimates of this parameter against 1+ population size lagged five years. This lag is the same as that used by Lett et al. (1979) and is considered reasonable on biological grounds since ages five and six contribute the most to the estimation of mean age at maturity (Bowen

et al 1981) and because sexual maturity is accelerated in direct proportion to juvenile growth rates (Laws, 1959). Estimates of population size from 1952 to 1976 are from sequential population analyses of Winters (1978) and, from 1977, from Shelton et al., (1996, revised). For population estimates prior to 1952 we used a linear extrapolation from the 1952 age 1+ estimate of Winters (1978). The relationship between 1+ population size (***P***) and mean age of maturity (***Mam***) is shown in Figure 7 and is described by the following linear regression (Table 2).

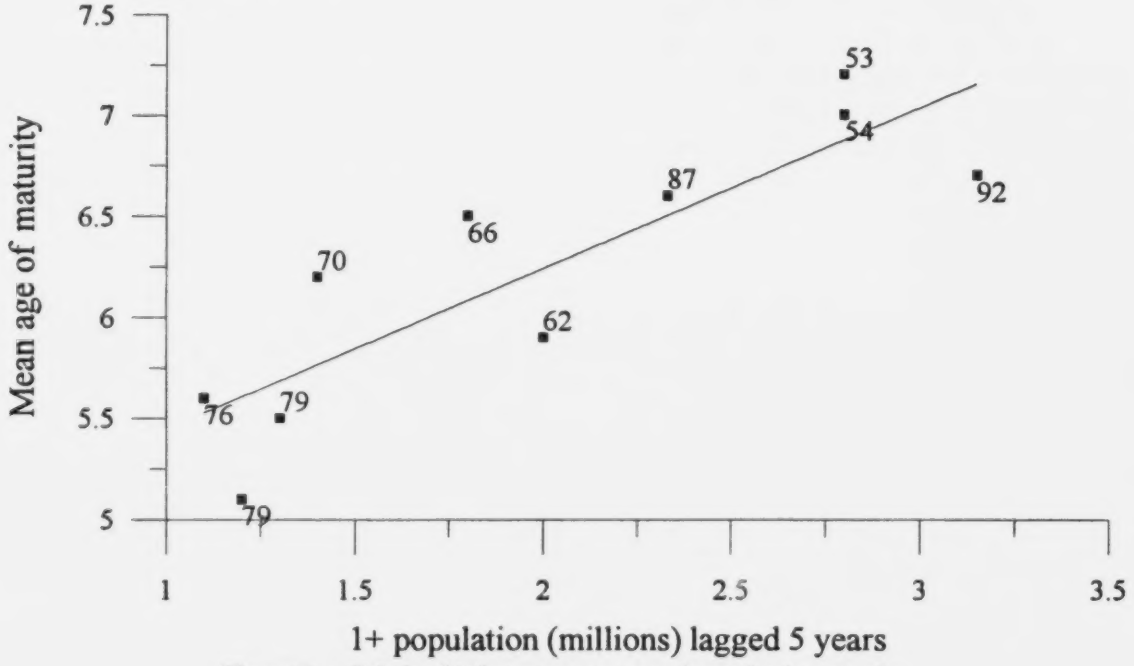

Figure 7. Relationship between mean age of reproductive maturity and age 1+ population lagged five years.

$$(2)\quad Mam_t = 4.66 + 7.92 \times 10^{-7} P_{1+_{t-5}}$$

where: Mam_t is the mean age of reproductive maturity in year t.
$P_{1+_{t-5}}$ is the 1+ population size lagged five years.

The relationship is highly significant (Table 2) and indicates that the mean age at maturity has a strong statistical link to population change. Consequently the proportion maturing at age a in year t can be obtained from the following algorithm.

$$(3)\quad Mat_{a,t} = \text{Sine}(38.2 + 17.1(a-(4.66 + 7.92 \times 10^{-7} P_{1+_{t-5}})))$$

The density dependent relationship of late term fertility rates (***Fr***) was investigated using age 2+ populations (P_{2+}) lagged one year (Lett and Benjaminsen, 1977). Lett and Benjaminsen (1977) excluded first year animals because this age-group was considered to have reduced competition with the rest of the herd, owing to spatial segregation during summer feeding. Bowen et al. (1981)

however, found no statistical reason to support this choice. The one year lag is considered appropriate given the severe depletion of energy reserves of adult females during lactation and hence, the per capita food supply during the post-weaning recovery period. The following linear relationship was found to best describe the response of late-term fertility rate to population change;

$$(4)\quad Fr_t = (106.2 - 1.01 \times 10^{-5} \times P_{2+_{t-1}}) / 100$$

where: Fr_t is the late term fertility rate in year t.
$P_{2+_{t-1}}$ is the 2+ population lagged one year.

The relationship is highly significant (Figure 8; Table 3) and shows that, over the past 30 years of data, fertility rate has responded inversely to population change. Taken together with the linear response in maturity rates to population change (Figure 7), we conclude there is strong statistical evidence of density-dependence in harp seals. The natural regulation of harp seals is achieved first and foremost by compensatory changes in overall reproductive rates as, indeed, they are for other marine and terrestrial mammals (Laws, 1959;Gambell, 1973; Margren,1963;Siniff et al., 1978).

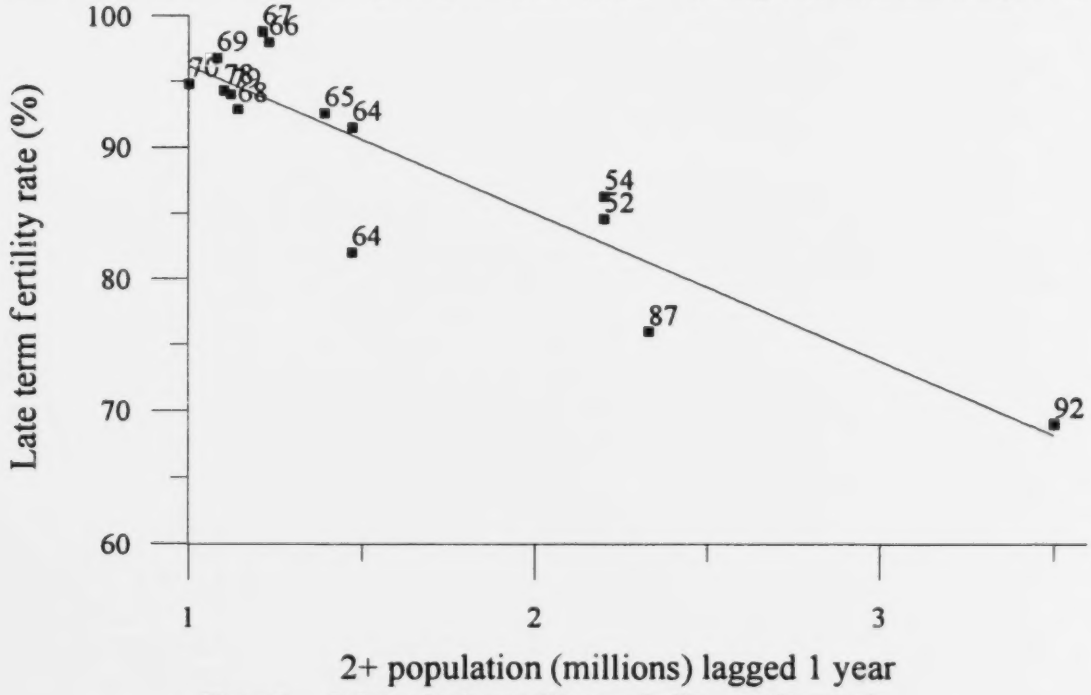

Figure 8. Relationship between late term fertility rate of harp seals and age 2+ population size lagged one year

Finally, annual pup production was determined by applying the above reproductive rates to the age-specific population numbers and accumulating across the mature age-groups as follows;

$$(5)\quad Pups_t = \sum_{a=1}^{30} Pop_{t,a}\, Fr_t\, Mat_{t,a}$$

where: $Pups_t$ is the pup production in year t.
$Pop_{t,a}$ is the population numbers of age a in year t.

3.0 CONSTRUCTION OF THE SIMULATION MODEL

The simulation model that we will use is similar to that described by Lett and Benjaminsen (1977) and modified by Lett et al. (1979). The model is stochastic and has two formulations, one density dependent and the other non-density dependent. The structure of the models are given in Figures 9 and 10 and detailed descriptions follow:

Starting input data: Starting population numbers at age, age specific selection factors, 1998 catch numbers at age, and the proportion of pups in the catch (1999 and beyond) are as described in the *Data sources and analytical procedures* section of this report. Normally distributed variance is applied to the starting population numbers and the natural mortality rate.

Non-density dependent model: In this model, it is assumed that recent reproductive rates (Sjare et. al 1996) and natural mortality rates (Shelton et al., 1996) are constant and apply for all catch equations. The user must specify the number of replicate runs and the number of years to project ahead for the model. Since the model is stochastic (takes into consideration the statistical variability in the parameter estimates), each run will be generated by randomly selecting from the normally distributed variance of the starting population numbers and the natural mortality rate. The population size at age is projected to the next year using the standard population equation of Pope (1972) :

$$N_{a,t+1} = (N_{a-1,t}\, e^{-m/2} - C_{a-1,t})\, e^{-m/2}$$

where $N_{a,t+1}$ = population number at age a in year t+1
$N_{a-1,t}$ = population number at age a-1 in year t
$C_{a-1,t}$ = catch at age a-1 in year t
m = instantaneous rate of natural mortality

Once the population size has been determined at age for year t+1, constant specified maturity and fertility rates at age are used to calculate the pup production which completes the population at age vector for year t+1. The estimated proportion of pups in the total catch, the completed population vector and age specific selection factors provide the basis for calculating the age specific catch in year t+1 as described in the *Data sources and analytical procedures* section of this report. This catch at age is used as input to the projection equation to continue the projection to year t+2. This iterative procedure is repeated for the requested number of years to project and for the requested number of replicate runs. The relevant statistics are compiled for each run from which the mean and standard deviations are calculated for pup production and population size.

Density dependent model: This model is identical in structure to the non-density dependent model but provision is made for the fertility rates and maturity rates to operate in a density-dependent manner. These rates are re-estimated for each years iteration forward in time. Derivation of these density dependent rates are described in the *Density dependent vital rates* section of this report.

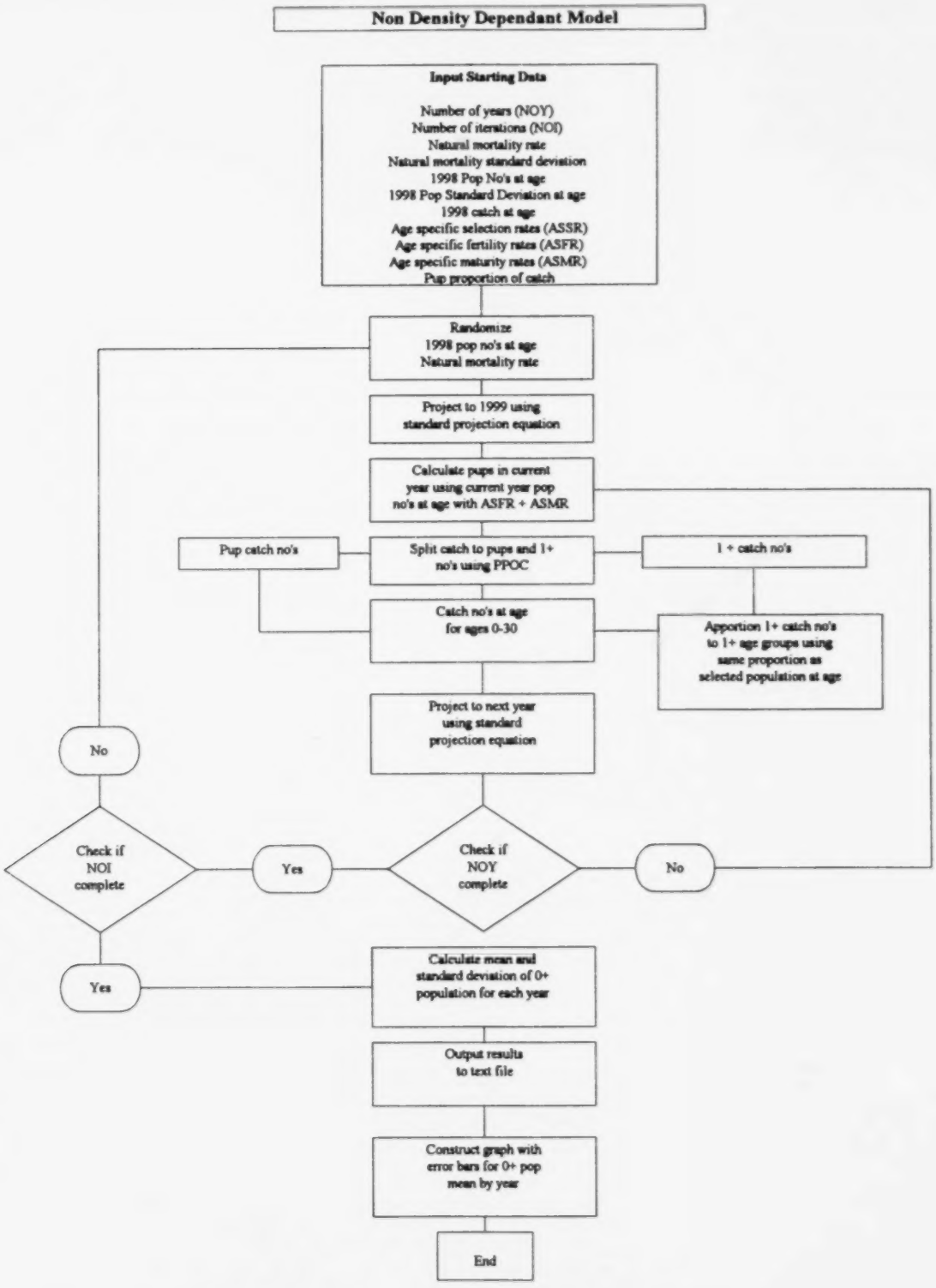
Non Density Dependant Model
Input Starting Data
Number of years (NOY)
Number of iterations (NOI)
Natural mortality rate
Natural mortality standard deviation
1998 Pop No's at age
1998 Pop Standard Deviation at age
1998 catch at age
Age specific selection rates (ASSR)
Age specific fertility rates (ASFR)
Age specific maturity rates (ASMR)
Pup proportion of catch
Randomize
1998 pop no's at age
Natural mortality rate
Project to 1999 using
standard projection equation
Calculate pups in current
year using current year pop
no's at age with ASFR + ASMR
Pup catch no's
Split catch to pups and 1+
no's using PPOC
1 + catch no's
Catch no's at age
for ages 0-30
Apportion 1+ catch no's
to 1+ age groups using
same proportion as
selected population at age
Project to next year
using standard
projection equation
No
Check if
NOI
complete
Yes
Check if
NOY
complete
No
Yes
Calculate mean and
standard deviation of 0+
population for each year
Output results
to text file
Construct graph with
error bars for 0+ pop
mean by year
End

Figure 9

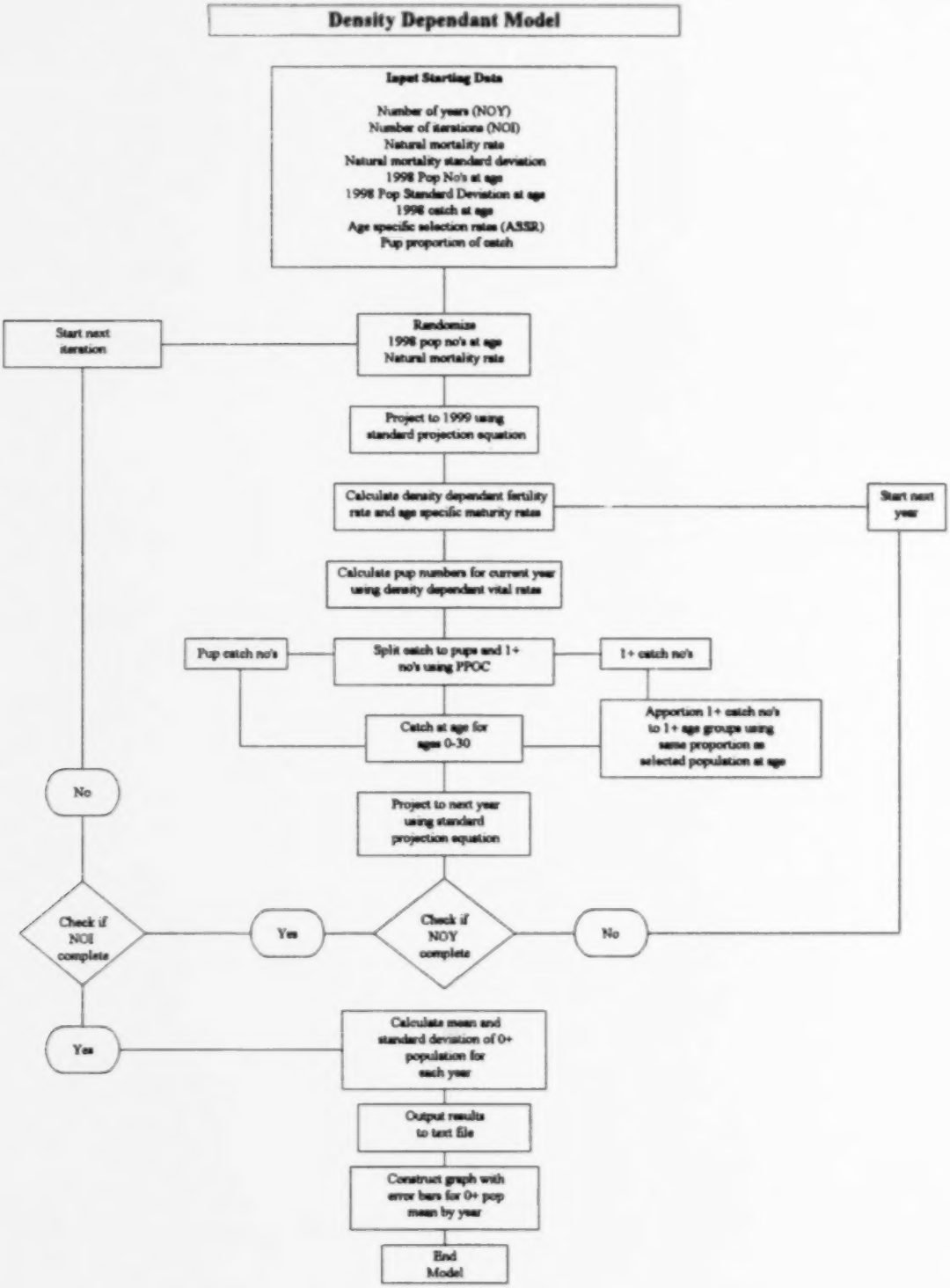
Density Dependant Model
Input Starting Data
Number of years (NOY)
Number of iterations (NOI)
Natural mortality rate
Natural mortality standard deviation
1998 Pop No's at age
1998 Pop Standard Deviation at age
1998 catch at age
Age specific selection rates (ASSR)
Pup proportion of catch
Randomize
1998 pop no's at age
Natural mortality rate
Start next iteration
Project to 1999 using standard projection equation
Calculate density dependant fertility rate and age specific maturity rates
Start next year
Calculate pup numbers for current year using density dependant vital rates
Pup catch no's
Split catch to pups and 1+ no's using PPOC
1+ catch no's
Apportion 1+ catch no's to 1+ age groups using same proportion as selected population at age
Catch at age for ages 0-30
Project to next year using standard projection equation
No
Check if NOI complete
Yes
Check if NOY complete
No
Yes
Calculate mean and standard deviation of 0+ population for each year
Output results to text file
Construct graph with error bars for 0+ pop mean by year
End Model

Figure 10

4.0 RESULTS OF SIMULATION STUDY

With respect to the study objectives (described above) we shall first describe results from the non-density dependent simulation model on the assumption that recent vital rates apply and remain constant during the entire simulation period. This will be followed by an alternative description of population response using the density-dependent formulation of the population model.

NON-DENSITY DEPENDENT RESULTS

Question 1. What is the current replacement yield?

The replacement yield for 1999 is estimated to be 402,000 animals based on a simple deterministic calculation using the revised output of the population assessment model of Shelton et al., (1996).

Question 2. What is the long-term response of the harp seal population if the hunt continues to be regulated at the current level of 275,000 seals?

In the absence of density-dependent controls, the harp seal population will increase in exponential fashion over the next 50 years (Figure 11), if the TAC remains at current levels of 275,000. Confidence limits on the estimates of the projected population size, representing a portion of the statistical error in the starting vectors, also increase with time.

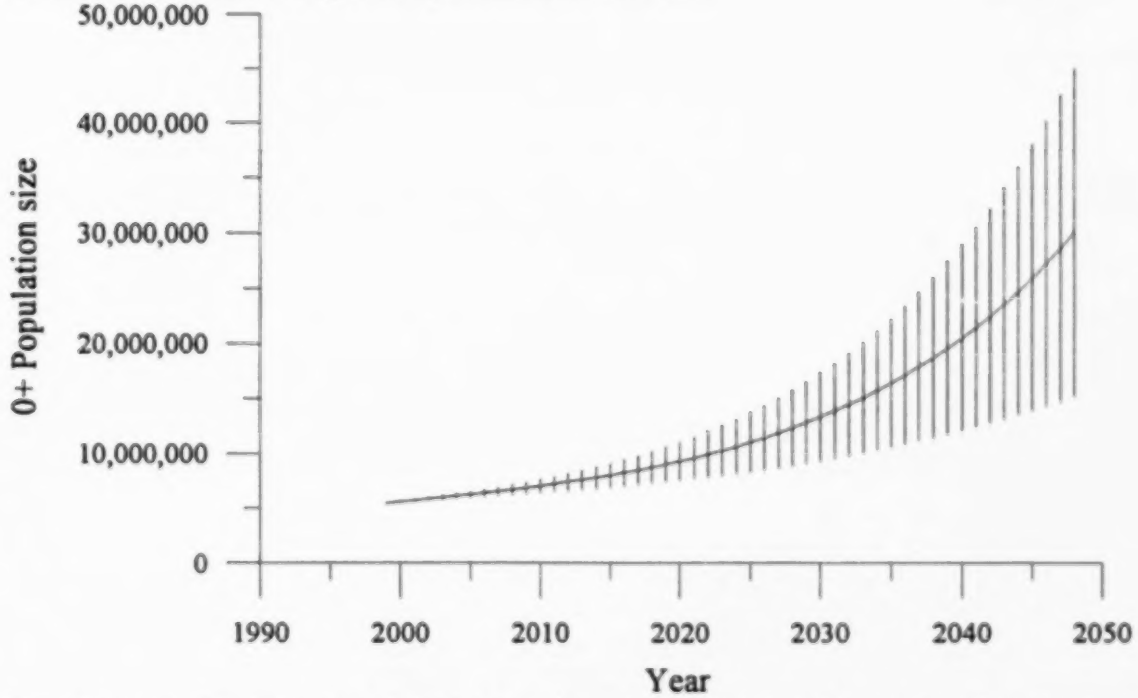

Figure 11. Simulated 50 year population trajectory (± one standard deviation) of harp seal population numbers for an annual catch of 275,000 seals (non-density dependent model)

Question 3. What is the long-term response of the harp seal population if the hunt is regulated at a level of 400,000 animals?

The long-term sustainable yield, at the current population size of harp seals, is estimated to be about 405,000 animals. In the absence of density-dependent controls, a harvest of 400,000 animals can therefore be sustained (Figure 12) with the population at the end of 50 years being slightly larger than the present level of 5.43 million (Figure 13) but with wide confidence limits.

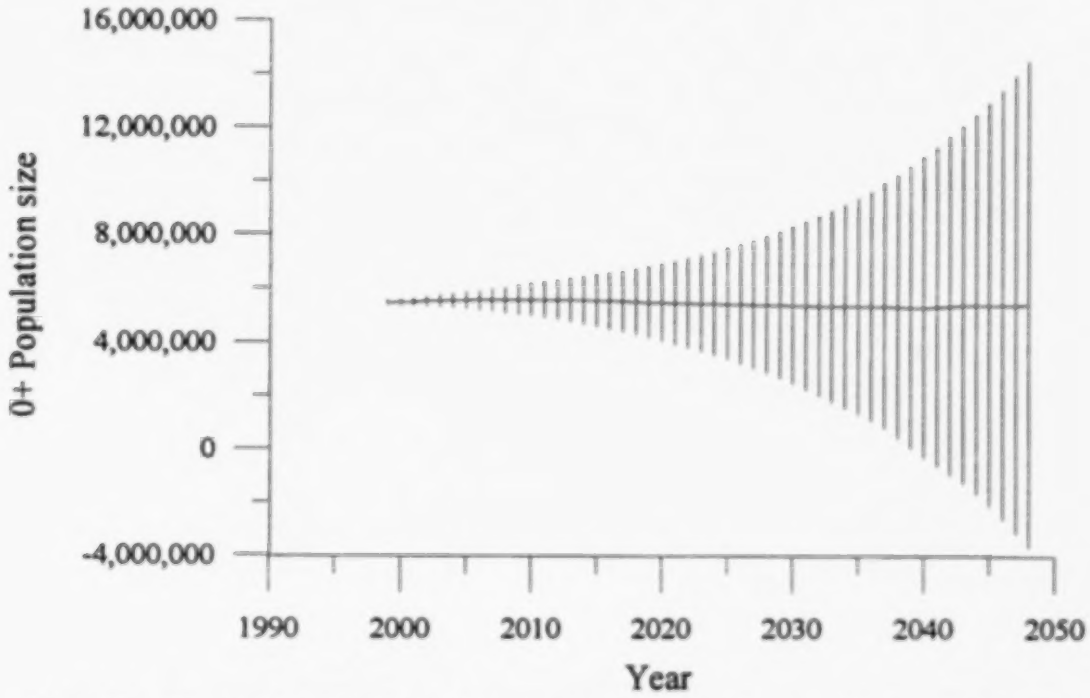

Figure 12. Simulated 50 year population trajectory (± one standard deviation) of harp seal population numbers for an annual catch of 400,000 seals (non-density dependent model)

Question 4. What is the long-term response of the harp seal population to a one-time cull of 2,000,000 animals followed by a resumption of the current harvest of 275,000 animals?

A one-time cull of 2,000,000 animals in the year 2000 in which the pup production is completely extirpated and the remainder taken as 1+ animals, will result in the harp seal population slowly recovering (Figure 14) and eventually, after 50 years, reaching a size of about 7.9 million animals (Figure 15). Confidence limits on this projection are large and do not exclude a population decline.

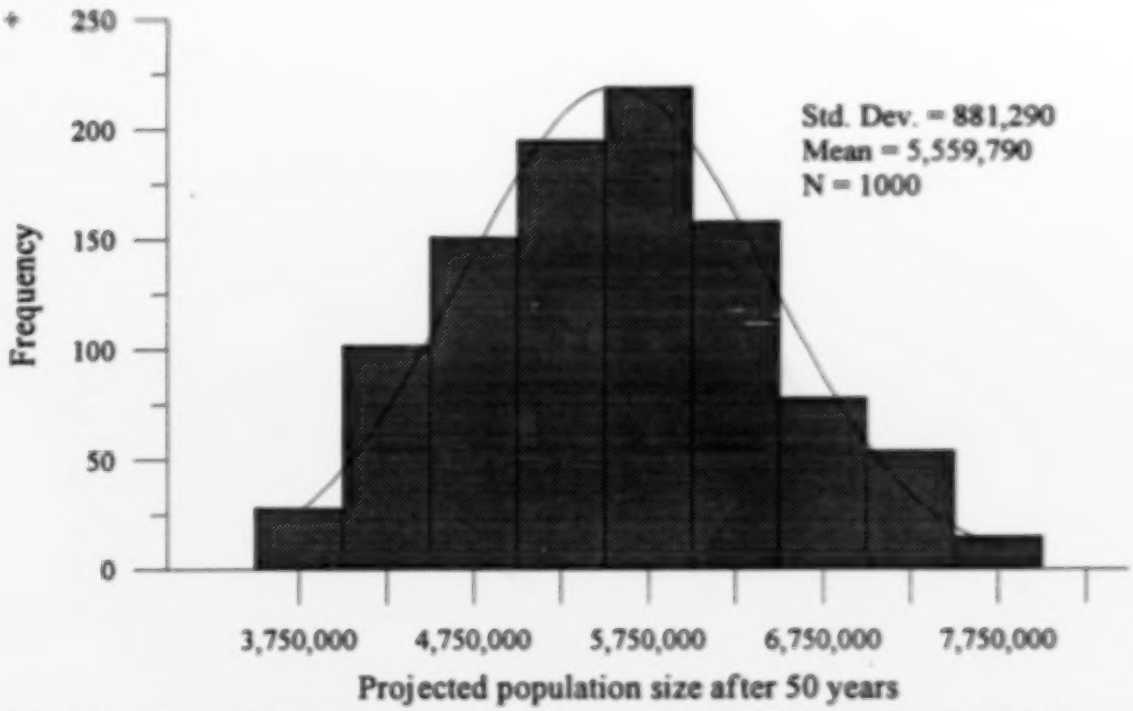

Figure 13. Frequency distribution of the means of 1000 runs (each run is 100 replicates) of 0+ population size projected 50 years for an annual catch of 400,000 seals (non-density dependent model)

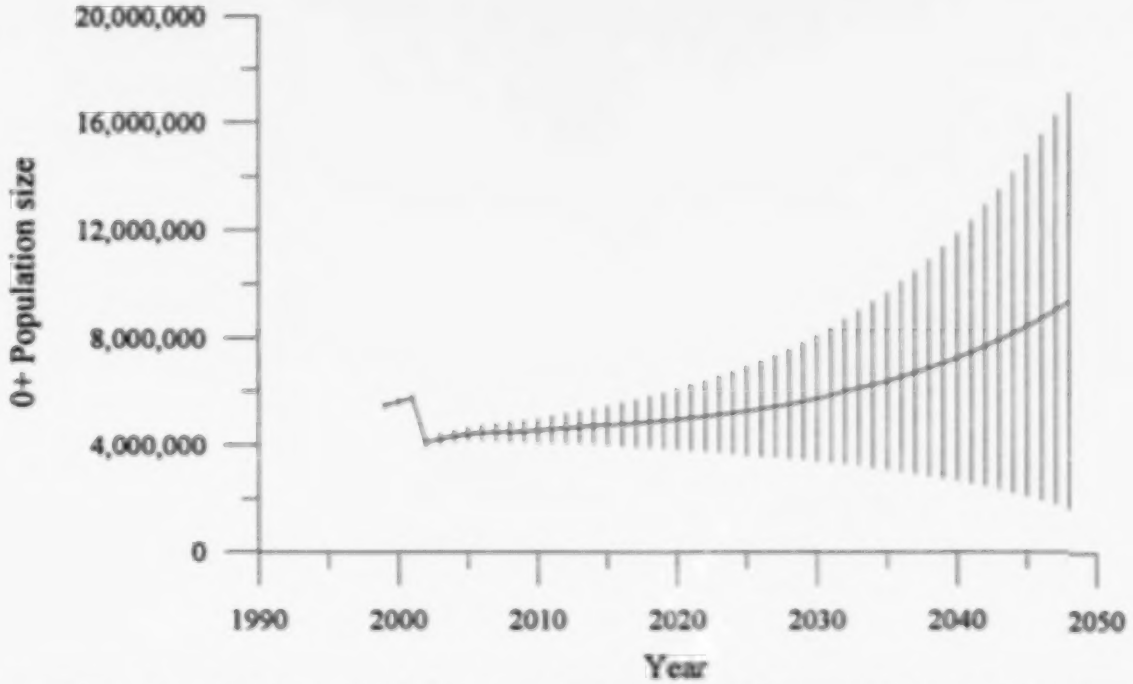

Figure 14. Simulated 50 year population trajectory (± one standard deviation) of harp seal population numbers for an annual catch of 275,000 seals following a one time cull of two million seals in the year 2000 (Non-density dependent model)

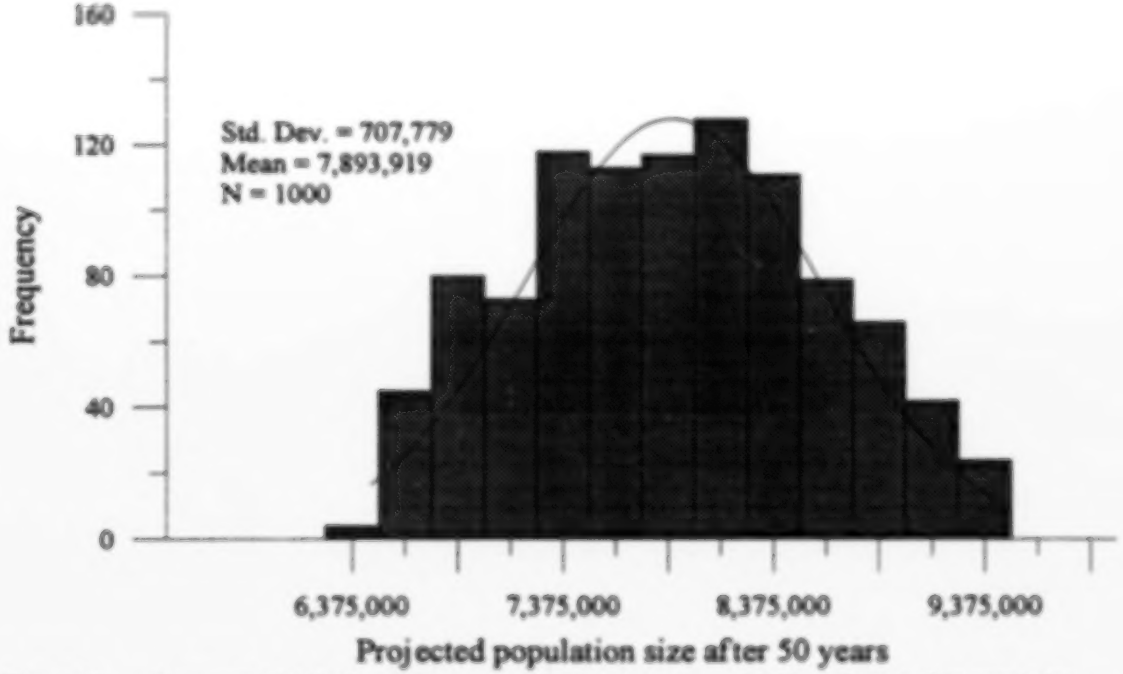

Figure 15. Frequency distribution of the means of 1000 runs (each run is 100 replicates) of 0+ population size projected 50 years for an annual catch of 275,000 seals and a one time cull of 2 million seals in the year 2000 (non-density dependent model)

DENSITY DEPENDENT RESULTS

Question 5. If a density-dependent function can be statistically demonstrated for the harp seal population, what is the maximum sustainable yield and at what population size will this maximum occur? How does the existence of density-dependence affect the conclusions arrived at with respect to the alternative harvesting strategies outlined above? Further, in the absence of a hunt how much farther will the population expand?

The historical data relating vital rates of harp seals to population change indicate that there is a strong statistical likelihood that reproductive rates act as natural regulators to counterbalance population changes in harp seals. A simulation model, incorporating the demonstrated statistical expressions of density-dependence, estimates that the maximum sustainable yield of harp seals is about 280,000 animals (Figure 16). The population size at which MSY occurs is not well defined because of the asymptotic nature of the yield curve but is in the range of 3.5 to 4.0 million animals, including pups.

With respect to *Question 1*, this is a short-term projection and consequently annual variability in vital rates may be as important to the calculation of replacement yield as the expected (lagged) density-dependent decline in vital rates. On average, however, reproductive rates would be expected to be

lower than observed during the early 1990's and therefore the replacement yield in 1999 may be somewhat lower than estimated.

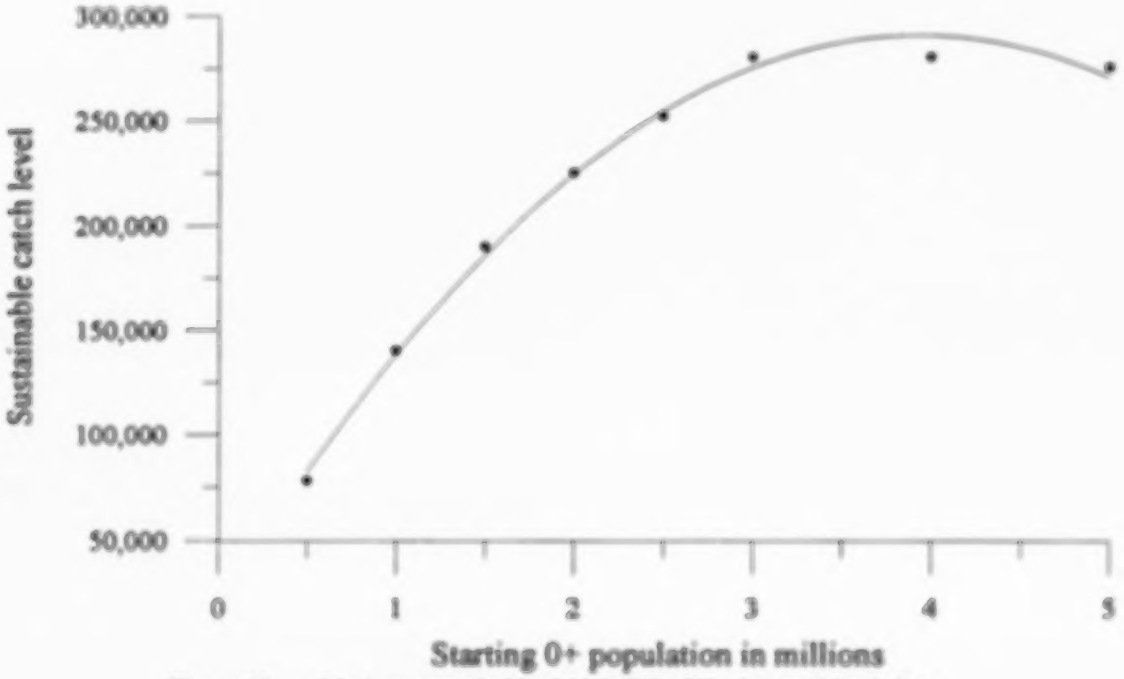

Figure 16. Maximum sustainable yield (MSY) of Northwest Atlantic harp seals as estimated by the density dependent model

With respect to ***Question 2***, a harvest of 275,000 animals can be sustained indefinitely as this is approximately the estimated MSY level. The harp seal population will gradually decline from current levels to the MSY population size over a period of several decades (Figure 17).

With respect to ***Question 3***, a harvest of 400,000 animals is above the MSY level and cannot be sustained over the long-term, if reproductive rates are density-dependent in the manner described. The population will be reduced to zero in the range of 30 to 40 years (Figure 18).

With respect to ***Question 4***, a one-time cull of 2,000,000 animals in the year 2000 will reduce the harp seal population to about 3,900,000 animals which is the approximate level of the MSY population size (Figure 19). A subsequent harvest of 275,000 animals will be sustainable and will stabilize the population at the MSY level.

With respect to ***Question 5***, in the absence of a hunt, the current population of 5.4 million seals will increase to a maximum level of 7.1 million seals (Figure 20) which, under the density dependent conditions described, represents the maximal or aboriginal population level, i.e. the maximum carrying capacity of the environment for this species under average condition observed in the past. At aboriginal levels the harp seal population is predicted to have a fertility rate of 47% and a mean age of reproductive maturity of 9.8 years.

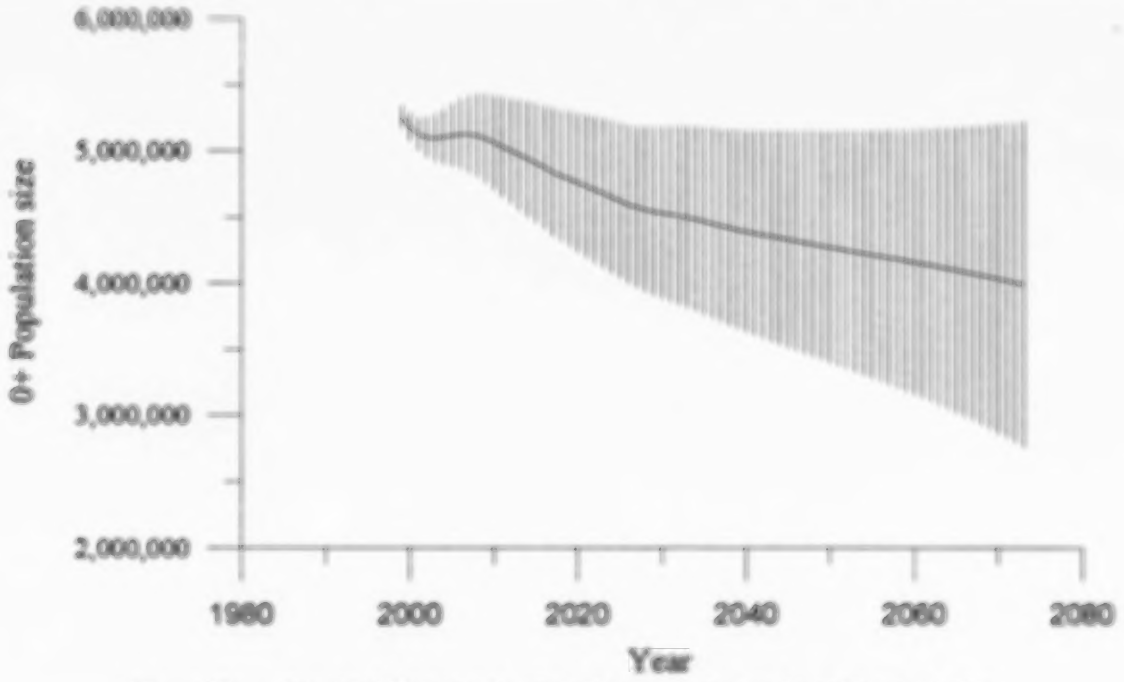

Figure 17. Simulated 75 year projection of 0+ population numbers of harp seals for an annual catch of 275,000 seals using the density dependent model

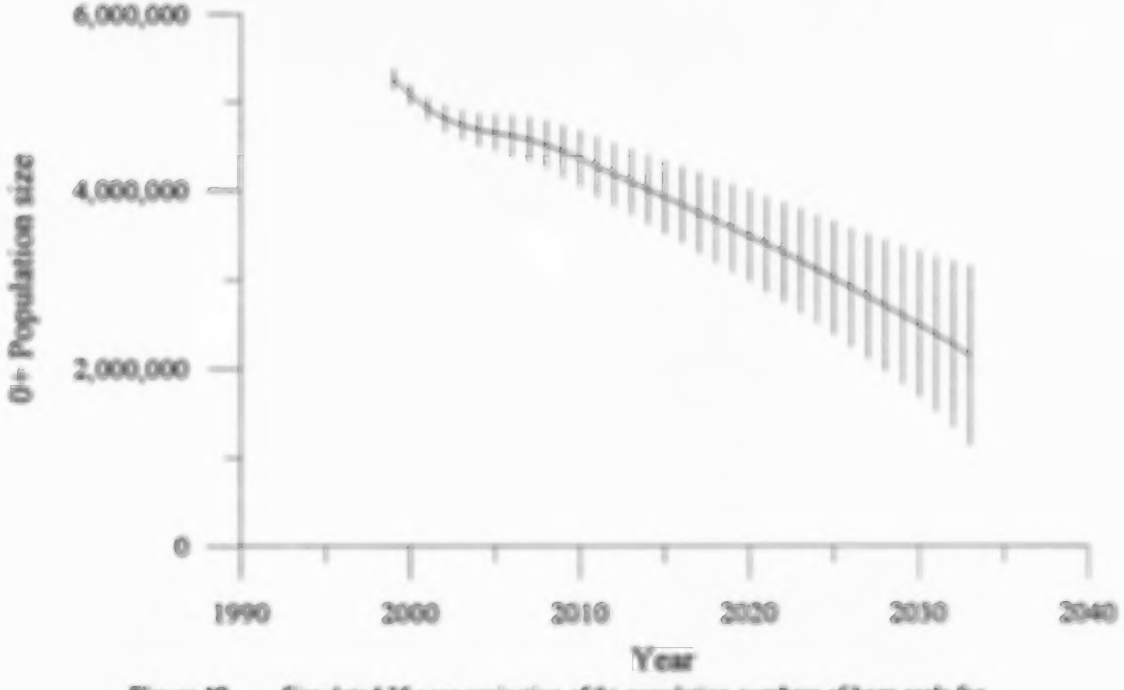

Figure 18. Simulated 35 year projection of 0+ population numbers of harp seals for an annual catch of 400,000 seals using the density dependent model

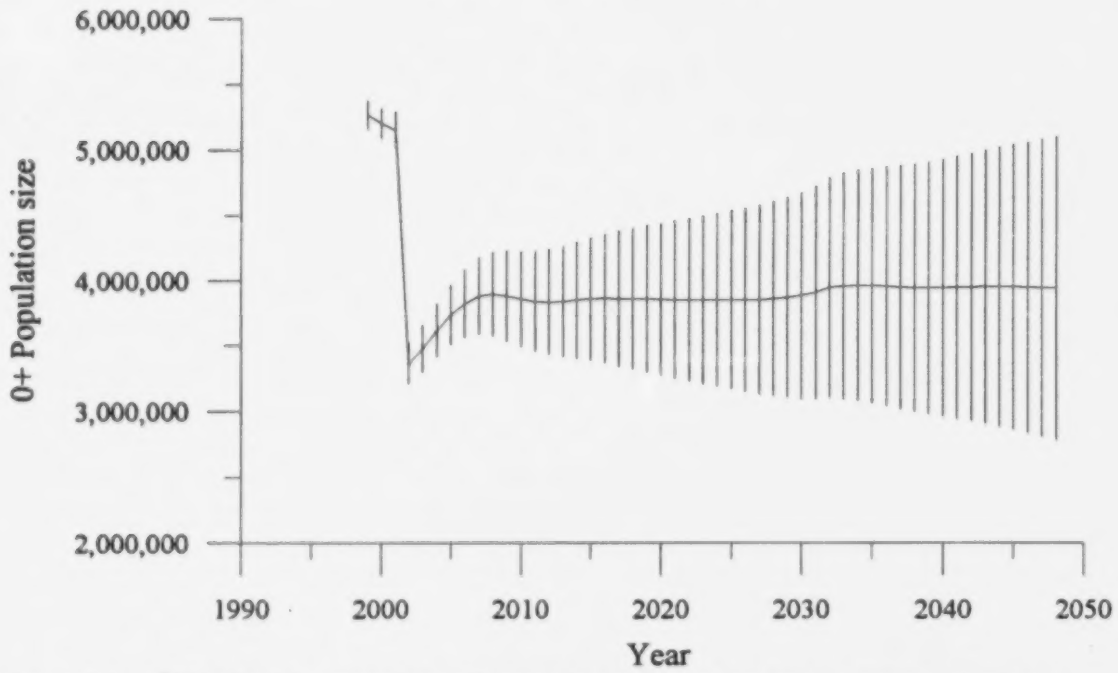

Figure 19. Simulated 50 year projection of 0+ population numbers of harp seals for an annual catch of 275,000 seals following a one time cull of 2,000,000 seals in the year 2000 using the density dependent model

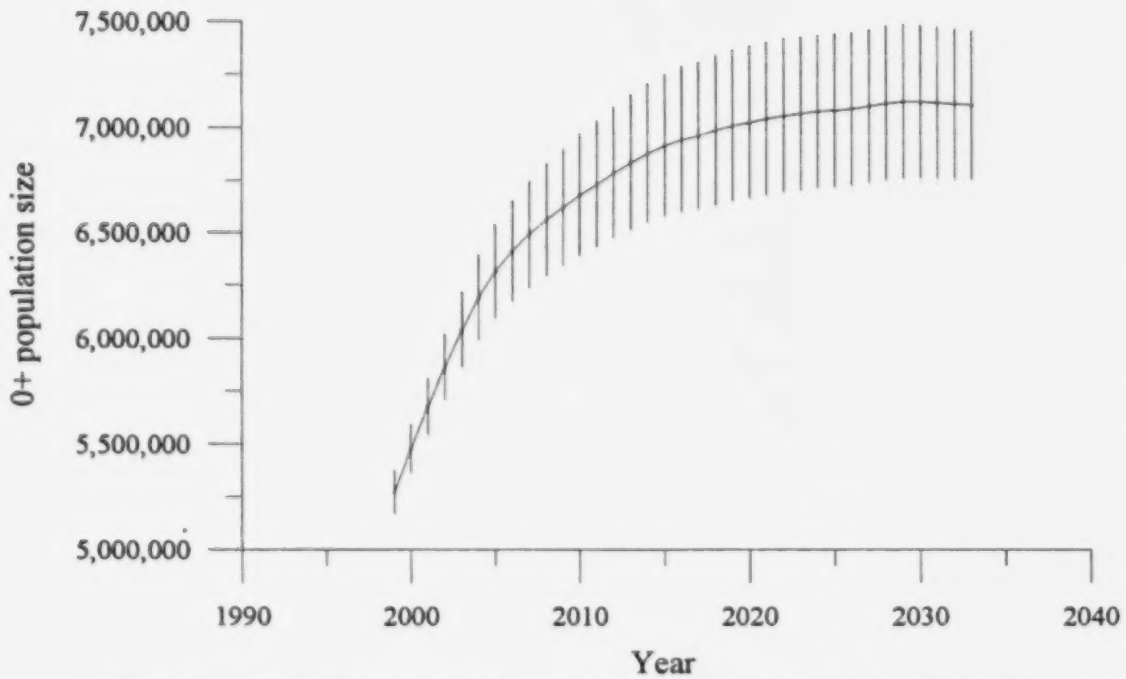

Figure 20. 50 year projection in the absence of any hunt using the density dependent model

5.0 DISCUSSION

The estimates of yield and population trajectories described above depend critically on the estimates of natural mortality (M) and reproductive rates used as input to the simulation models. Consequently, uncertainties in these parameters will affect the confidence with which our conclusions are derived. We shall deal first with the natural mortality estimate.

Natural mortality is difficult to estimate for most wild populations, particularly on an annual basis. For this reason, natural mortality is usually estimated from a time series of empirical population estimates or indices. We use a value of M=0.087 which is the mean value derived by Shelton et al., (1996, revised) as providing the best fit to a population model describing the change in pup production from 1978-93 by mark-recapture methods, to estimates of pup production from aerial surveys in 1990 and 1994. As calculated, M includes all sources of mortality other than the reported catch and is in the middle of the range of M values ($0.075 < M < 0.11$) reported in the literature for Northwest Atlantic harp seals by a variety of methods, not all of which are independent or of equal reliability. From this perspective and taking into account central tendency, the value of M used in this report is probably close to the population value. However, we consider that if there is a bias in the estimated value of M by Shelton et al., (1996, revised) it is likely on the high side for several reasons. For example, Roff and Bowen (1983), using a similar population model but calibrated to an estimate of pup production for 1967, estimated a value of M=0.075. Including the 1967 data point in the population model of Shelton et al.,(1996) would likely decrease their maximum likelihood estimate of M to some value intermediate between 0.087 and 0.075. Further, aerial surveys are more likely to underestimate than overestimate pup production. This is because it is never certain that all breeding patches have been located and counted (Anon., 1985). Sergeant (1991) cites two examples (1964, 1983) in which aerial census results significantly underestimated pup productions estimated from mark-recapture experiments for the same year. Any underestimation of the aerial survey estimates for 1990 and 1994 used to calibrate the population model of Shelton et al., (1996) will result in a over estimate of M and an underestimate of the 1+ population size in 1998. If natural mortality is lower than that used in this report then our estimates of harvest levels will be underestimated and the simulated population response times to various harvest strategies will be overestimated.

With respect to reproductive rates, the fertility rates used in this report are likely to be reliably estimated since they are not age-dependent and therefore less affected by poor sampling for particular age -groups. The mean age of maturity estimates for the 1990's, however, are significantly below the expected estimate from the regression line (Figure 7) describing the relationship between maturity and population size. This may reflect a temporary increase in the carrying capacity of the environment for harp seals during the 1990's which would affect their per capita food supply, in addition to population density. For example, the decline in the ground fish biomass has a statistical inverse relationship win increases in prey species such as caplin and shrimp which are also important in the diet of harp seals. In the Pacific a ground fish-marine mammal competition for common prey has been associated with changes in the population stellar sea-lions (Merrick, 1997). However, sampling data on which the 1990's maturity rates are based (Sjare et al.,1996) are insufficient on an annual basis, particularly for the critical age-groups (ages five and six) affecting the estimate of mean age at maturity. Aggregating these over several years, as Sjare et al.,(1996) have done, certainly improves the estimates but may obscure short-term changes in maturity rates. If the mean age at maturity for

the 1990's is higher than that used in this report, then projected yield levels will be over-estimated for the non density-dependent formulation of the simulation model.

This report describes the northwest Atlantic harp seal population as having an MSY harvest of about 280,000 animals from a MSY population size in the range of 3.5 to 4.0 million animals. Previous estimates of the MSY harvest level for this population overlap this estimate. Lett and Benjaminsen (1977) indicated that the MSY is about 240,000 animals from a total population size of about 2.0 million animals, if fertility and maturity rates are density dependent and M=0.114. Lett et al . (1979) modified this estimate to a MSY harvest of 230,000 animals at a total population size of about 3.0 million under a scenario of density-dependent fertility and maturity and M=0.10. Winters (1978) estimated the MSY harvest level to be 290,000 animals from a total population of about 2.3 million animals using a value of M=0.098 and a density-dependent maturity rate. Barchard (1978) used long-term catch statistics and estimated the MSY catch to be 244,000 animals from a total population of about 2.5 million animals. It is evident that the range of estimates for the MSY harvest level is much smaller than for the population level at which that MSY production occurs. This is because the degree of density-dependence can have a substantial effect on the shape of the surplus production curve describing the relationship between pup production and total population size (Lett et al., 1979). Consequently, it is much more difficult to reliably estimate the stock size that corresponds to the MSY harvest level than it is to estimate the MSY harvest level itself. However, our estimate of the approximate MSY stock size is about 50% of the unexploited level of about 7.1 million animals, which is consistent with theoretical expectations from the surplus production model of Shaefer (1954), and observations from other marine mammal populations (Anon., 1985).

Insofar as maximal population size is concerned, the estimate of 7.1 million harp seals in this report is much larger than previous estimates from the published literature. Winters (1978) estimated the aboriginal population size to be 4.2 million animals of all ages based on a Graham-Shaefer plot of per capita pup production. Lett and Benjaminson (1977) provided an estimate of 3.7 million seals from a population model which included several density-dependent functions. Lett et al. (1979) re-estimated the aboriginal population size to be 5.5 million animals of all ages using a population model with density-dependent pregnancy and maturity rates. Barchard (1978) conducted a detailed analysis of standardized catch and effort data of the harp seal hunt going back to the beginning of the hunt in the late 18th century. From these data the maximal equilibrium herd size was estimated to be 4.1 million animals at the beginning of the seal fishery in the late 18th century. Nearly all of these estimates have been eclipsed by the size of the current population of 5.4 million animals as estimated by Shelton et al., (1996, revised). Indeed, a strong argument can be made that the current herd size is probably the largest since the beginning of the commercial seal hunt in the late 18th century. Retrospective estimates of the harp seal population during the early 1950's are in the range 3.0 to 3.5 million seals (Winters, 1978; Lett and Benjaminson, 1977). This agrees quite well with aerial survey estimates of about 3.25 million seals in 1950-51 (Fisher, 1954). The commercial seal hunt was just resuming at this time following almost complete cessation during the Second World War. This hiatus that would not have been fully felt in the breeding stock until the late 1940's and early 1950's as the 1941-45 yearclasses began entering their substantive breeding ages. Further, an examination of the smoothed catches going back to the early 19th century (Barchard, 1978) shows a downward cascade which was not reversed until after the Second World War, indicating that the harp seal herd was below sustainable harvest levels throughout the early part of the 20th century. Barchard (1978) proceeded

to develop a standardized time series of catch/effort statistics from which he concluded that the harp seal population had recovered to near maximal levels by the end of the Second World War. Yet, current population levels of harp seals are 50% higher than estimated levels in the early 1950's when, as stated above, the breeding stock would still have been expanding as a result of the recruitment of the 1941-45 year classes. This is perhaps the best empirical evidence which places the current population of harp seals at or near the zenith of its historical population trajectory and explains the reduced growth rates and severe reproductive stress that is evident in its very low fertility rates and elevated age at reproductive maturity.

From a productivity point of view, the greatest sustained harvest of seals (MSY) is as much a desirable biological objective as it is a management objective. The harp seal population at its current level is reproductively stressed with fertility rates below 70% and a maturity rate at the upper end of the observed range. Also, Chabot et al., (1996) found that young female harp seals grew more slowly in both length and mass during the period 1990-94 than previous observations for the 1970's and 1980's. Reducing the harp seal population to the MSY stock level (3.5-4.0 million seals) should invoke density-dependent improvements in both harp seal growth and reproductive rates to more optimum levels. Further, from an ecosystem viewpoint harp seals are apex predators which convert prey production to seal biomass at a low growth efficiencies (Slobodkin, 1962). For example, the consumption statistics given in Stenson et al. (1997) indicate that 450,000 tons (assuming a mean weight of 100 kg per seal) of harp seals consumed about 7.0 million tons of food in 1994, which resulted in a net surplus production (i.e. replacement yield) of only about 15,000 tons (at 50 kg per seal). A similar biomass of cod would, from simple yield per recruit calculations, produce about 100,000 tons of sustainable yield from a total food consumption of only 1.6 million tons of prey (Jones and Richards,1976). That is to say, overall productivity of the ecosystem could improve by reducing the seal population to some lower level such as the MSY level and allowing the excess production to be consumed by lower level predators (such as fish) which have higher gross growth efficiencies. In addition, a reduced number of harp seals may enhance the probability of recovery of depressed groundfish populations such as northern cod which continue to form a significant component of the harp seal diet and are also major competitors with seals for a variety of common prey species such as capelin.

Management of the harp seal population at the MSY stock size estimated in this report would not entail a significant increase in the risk of sustained overexploitation. This is because seal populations have an extended age structure which acts as a buffer to normal population perturbations. Consequently, seal populations change so slowly that routine population monitoring (such as that already in place) should detect any significant anomalies in population levels. For example, the harp seal population declined from about 3.0 million seals in the early 1950's to about 1.5 million in the early 1970's (Winters, 1978). This is a decline of about 3.5 % per year during a period in which the hunt was unregulated by quotas and included an extended period (to 1961) when large numbers of breeding females were harvested. Current aerial surveys have a coefficient of variation of about 8-9% and are conducted every four years; i.e. they are clearly capable of detecting any major changes in seal abundance.

Finally, a significant finding of this study is that increases in reproductive performance that accompanied the decline of harp seals from the early 1950's to the 1970's has been reversed during

the expansion of the herd since then. This is clear confirmation that such rates are density-dependent in this population as they are in many other wild populations. This means that the population projections by the density-dependent simulation model are likely to be much more realistic than those from the non-density dependent model. Both models assume that average conditions in the future are the same as those which determined the vital rates in the past. The veracity of this assumption can only be tested by the passage of time and the accumulation of new data on population numbers and associated vital rates.

6.0 SUMMARY

(1) The harp seal population, currently estimated at 5.4 million seals, has more than tripled since the imposition of annual quotas in 1971 and is about 50% higher than population estimates for the early 1950's ,when the harp seal population was considered to have recovered to near maximal population levels. Current population size has eclipsed nearly all previous estimates of maximal population size; it is quite probable that the harp seal population is now at its highest level since the development of the commercial seal hunt in the early part of the 19th century.

(2) The current management regime for harp seals is based on periodic updates of replacement yield, defined as that level of annual catch which stabilizes the population from one year to the next. This strategy is appropriate only when the regulated population has reached the long-term management objective. In the case of harp seals, there appears to be no long-term management objective with respect to desired population levels. In this report a variety of alternative harvesting strategies are considered and the population response of harp seals to these strategies are simulated using two population models.

(3) Analysis of long-term changes in harp seal fertility and maturation rates shows substantial variations which we have shown to have a strong statistical link with changing population levels. We have concluded that the harp seal herd is now reproductively stressed and that this has been due to density-dependent changes as a result of the current high population levels. The published literature indicates that the harp seal population is also experiencing sub-optimal somatic growth rates (growth in flesh as opposed to gonads), likely another population response to its current high levels of abundance.

(4) Significant findings of the simulation studies are as follows;

(a) the replacement yield for 1999 is 402,000 animals, if recent mortality and reproductive rates hold.

(b) the maximum sustainable yield (MSY) is estimated to be about 280,000 seals at an MSY population level of about 3.5 to 4.0 million animals.

(c) a one-time cull of 2.0 million animals in the year 2000 would reduce the population to the approximate level of the MSY population, after which a long-term harvest of 275,000 animals could be sustained under normal environmental conditions.

(d) alternative harvest levels such as a kill of 400,000 seals will gradually reduce the current population to the MSY level over a period of several decades.

(e) in the absence of a commercial hunt the harp seal population will gradually increase to a maximal level of 7.1 million animals.

(5) Regulation of the harp seal population at the MSY population level should be considered as a management option for a variety of biological and conservation benefits such as optimizing harp

seal reproductive and growth rates, improving overall ecosystem yield and increasing the probability of recovery of depressed groundfish populations.

Appendix I
References

Anon., 1979 . International workshop on biology and management of Northwest Atlantic harp seals. workshop report, 3-6 December, 1979.

Anon., 1985. Seals and Sealing in Canada. Report of the Royal Commission, Vol. 3.

Anon., 1998. Report of the Joint ICES / NAFO Working Group on Harp and Hooded Seals. NAFO SCS Doc. 98/16.

Barchard, W.W., 1978. Estimates of historical stock for Northwest Atlantic harp seals, *Pagophilus groenlandicus*. M.Sc thesis, University of Guelph, 164 p.

Bowen, W. D., C.K. Capstick and D. E. Sergeant, 1981. Temporal changes in the reproductive potential of female harp seals, *Pagophilus groenlandicus*. Can. J. Fish. Aquat. Sci. 40: 728-743.

Chabot, D., G. B. Stenson and N. G. Cadigan, 1996. Short and long- term fluctuations in the size and condition of harp seal (*Phoca groenlandica*) in the Northwest Atlantic.NAFO Sci. Counc. Studies, 26;15-32.

Chafe, L. G., W. A. Mann and H. M. Mosdell, 1923. Chafe's Sealing Book: A history of the Newfoundland seal fishery from the earliest available records down to and including the voyage of 1923. The Trade Printers and Publishers Ltd., St. John's, Nfld. 105 p.

Coleman, S. J., 1937. The present state of the seal fishery. Jour. Anim. Ecol. 6: 145-159.

Cooke, J. G., 1986. Estimation of harp seal pup production from samples. Can. J. Fish. Aquat. Sci., 42:468-473.

Fisher, H. D., 1954. Studies on the reproduction in the harp seal in the Northwest Atlantic. Fish. Res. Bd. Can. MS Report 588: 109 p.

Jones, R. and J. Richards, 1976. Some observations on the interrelationships between major fish species in the North Sea. ICES C.M. 1976/F:36.

Gambell, R., 1973. Some effects of exploitation on reproduction in whales. Jour. Reprod. Fertil. Suppl., 19:533-553.

Kapel, F. O., 1996. Recoveries in Greenland, 1949-94 of tagged or branded harp and hooded seals. NAFO Sci. Coun. Studies 26: 87-100.

Laws, R. M., 1959. Accelerated growth in seals with special reference to the Phocidae. Norsk Hvalfangst-tid., 48: 42-45.

Lett, P. F. and Benjaminson, 1977. A stochastic model for the management of the Northwest Atlantic harp seal population. J. Fish. Res. Bd. Can.34:1155-1187.

Lett, P. F., R. K. Mohn and D. F. Gray, 1979. Density-dependent processes and management Strategy for the Northwest Atlantic harp seal population. ICNAF selected papers no. 5:61-80.

Markgren, G., 1969. Reproduction of moose in Sweden. Viltrevy (Stockholm), 6 (3):125-133.

Merrick, R. L., 1977. Current and historical roles of apex predators in the Bering Sea ecosystem. J. Northw. Atl. Fish. Vol. 22: 343-356.

Pope, J. G., 1972. An investigation into the accuracy of the virtual population analysis using cohort analysis. ICNAF Res. Bull., No. 9:65-74.

Roff, D. A. and W. D. Bowen, 1983. Population dynamics and management of the Northwest Atlantic harp seal. Can. J. Fish. Aquat. Sci., 40:919-932.

Roff, D. A. and W. D. Bowen, 1986. Further analysis of population trends in the Northwest Atlantic seal population from 1967 to 1985. Ca. J. Fish. Aquat. Sci., 43:553-564.

Sergeant, D. E., 1971. Calculation of the production of harp seals in the Northwest Atlantic. ICNAF Redbook 1971, Part III:157-184.

Sergeant, D. E., 1973. Feeding, growth, and productivity of Northwest Atlantic harp seals. J. Fish. Res. Bd. Can. 30:17-29.

Sergeant, D. E., 1975. Estimating numbers of harp seals. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 169:274-280.

Sergeant, D. E., 1977. Studies on harp seals of the western North Atlantic population in 1977. ICNAF Res. Doc. 77/XI/58.

Sergeant, D. E., 1978. Research on harp seals in 1978. ICNAF Res. Doc. 76/X/ 85.

Sergeant, D. E., 1991. Harp seals, man and ice. Can. Spec. Publ. Fish. Aquat. Sci. 114. 153 p.

Schaefer, M. B., 1954. Some aspects of the dynamics important to the management of the commercial marine fisheries. Bull. Amer. Trop. Tuna Comm., 1 (2):26-56.

Shelton, P. A., G. B. Stenson, B. Sjare, and W. G. Warren, 1996. Model Estimates of harp seal numbers at age for the Northwest Atlantic. NAFO Sci. Counc. Studies 26:1-14.

Sjare, B., G. B. Stenson and W. G. Warren, 1996. Summary of female harp seal reproductive parameters in the Northwest Atlantic. 1996. NAFO Sci. Counc. Studies 26: 41-46.

Slobodkin, L. B., 1962. Energy in animal ecology. Adv. Ecol. Res. 1: 69-101.

Siniff, D. B., I. Sterling and L. L. Eberhardt, 1978. Problems in the conservation of polar marine mammals. Ch. 7, p. 161-173. In M. A. Whinnie (ed). Polar Research: to the present and future., Westview, Boulder, Col. AAAS Sel. Symp. Ser. 7.

Stenson, G. B. and B. Sjare, 1997. Seasonal distribution of harp seals in the Northwest Atlantic. ICES C. M. Doc., No. CC:10.

Stenson, G. B., M. O. Hammill and J. W. Lawson, 1997. Predation by harp seals in Atlantic Canada: preliminary consumption estimates for arctic cod, capelin and atlantic cod. J. Northw. Atl. Fish. Sci., Vol.22 :137-154.

Warren, W. G., P. A. Shelton and G. Stenson, 1997. Quantifying some of the major sources of uncertainties associated with the estimates of harp seal prey consumption part 1: Uncertainties in the estimates of harp seal population size. J. Northw. Atl. Fish. Sci., vol 22 :289-302.

Winters, G., 1978. Production, mortality and sustainable yield of Northwest Atlantic harp seals (*Pagophilus groenlandicus*). J. Fish. Res. Bd. Can., 35:1249-1261.

Yablokov, A. V. and D. E. Sergeant, 1963. Cranial variations in the harp seal. Zool. Zh 42 : 1857-1862.

Focus

Appendix II
Tables

Table 1. Regression results for arcsine maturity rate versus standardized age

```
Multiple R              .95684
R Square                .91554
Adjusted R Square       .91085
Standard Error         8.07797

Analysis of Variance:

                DF    Sum of Squares      Mean Square

Regression       1         12732.144        12732.144
Residuals       18          1174.566           65.254

F =     195.11768          Signif F              .0000

Variables in the Equation

Variable                     B         SE B       Beta           T Sig T

STAGE                17.120576     1.225660    .956838        13.968.0000
(Constant)           38.197871     1.827220                   20.905.0000
```

Table 2. Regression results for mean age at maturity versus 1+ population lagged 5 years

```
Multiple R                .86042
R Square                  .74032
Adjusted R Square         .70786
Standard Error            .37278

Analysis of Variance:

                DF   Sum of Squares      Mean Square

Regression       1        3.1692925        3.1692925
Residuals        8        1.1117075         .1389634

F =      22.80666          Signif F              .0014

Variables in the Equation

Variable                     B         SE B       Beta           T Sig T

ONEPSMIL      7.922042958-07  1.65888-07    .860416         4.776.0014
(Constant)          4.655098     .350215                   13.292.0000
```

Focus

Table 3. Regression results for fertility rate versus 2+ population lagged one year

Multiple R	.90277
R Square	.81500
Adjusted R Square	.79958
Standard Error	3.58887

Analysis of Variance:

	DF	Sum of Squares	Mean Square
Regression	1	680.89450	680.89450
Residuals	12	154.55979	12.87998

F = 52.86455 Signif F = .0000

Variables in the Equation

Variable	B	SE B	Beta	T	Sig T
2+ pop_{t-1}	-1.01097277E-05	1.39058E-06	-.902773	-7.271	.0000
(Constant)	106.175094	2.417217		43.925	.0000